Equus stenonis from the middle Villafranchian locality of Volax (Macedonia, Greece)

George D. KOUFOS & Theodora VLACHOU
Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki,
54006 Thessaloniki (Greece)

Koufos G. D. & Vlachou T. 1997. — *Equus Stenonis* from the middle Villafranchian locality of Volax (Macedonia, Greece). *Geodiversitas* 19 (3) : 641-657.

ABSTRACT
The locality of Volax is situated in eastern Macedonia, Greece, in a small karstic-tectonic basin. The Volax horse is a large-sized horse with moderately plicated enamel in the upper teeth, short protocone with flat lingual border, hypsodont teeth, slightly plicated flexids in the lower teeth, as well as short and robust metapodials. The dental and postcranial characters of the Volax horse indicate that it is a stenonoid horse with greatest similarities to the horse from Dafnero (Greece) and La Puebla (Spain). It is also close to *E. s. vireti* from Saint-Vallier, as well as to the horse from Olivola and Matassino (Italy). The study of the Volax equid adds to our knowledge about the Villafranchian horses and their relationships. The age of the Volax locality is also discussed and a middle Villafranchian age (MN17) is proposed.

KEY WORDS
mammalia,
Equidae,
middle Villafranchian,
Macedonia,
Greece.

RÉSUMÉ
Le gisement fossilifère de Volax se situe en Grèce, dans la Macédoine orientale. Le matériel d'équidé trouvé dans ce gisement fait l'objet de ce travail. Il s'agit d'un équidé de grand taille, à l'émail de la denture supérieure modérément plissé, doté d'un court protocône et d'une face linguale plate, d'une hypsodontie assez forte. Les flexides de la denture inférieure sont légèrement plissés, les métapodiaux courts et robustes. Ces caractéristiques montrent de fortes similitudes avec *E. s. vireti* des gisements de Dafnero (Grèce) et de La Puebla (Espagne). L'équidé de Volax ressemble aussi à *E. stenonis* de Saint-Vallier, et à l'équidé d'Olivola et de Matassino (Italie). L'étude des équidés de Volax parfait notre connaissance des chevaux du Villafranchien et de leurs relations de parenté. La datation du gisement est également discutée ; un âge Villafranchien moyen (MN17) peut être proposé.

MOTS CLÉS
mammifères,
équidés,
Villafranchien moyen,
Macédoine,
Grèce.

INTRODUCTION

The locality of Volax has been discovered in 1961 by Prof. H. J. Martini (University of Hannover), who investigated the area studying the manganium deposits and informed Prof. O. Sickenberg, of the same University, about the new locality. With the permission of Prof. M. Mitzopoulos (University of Athens) and Prof. G. Matinos (University of Thessaloniki), Sickenberg excavated and collected abundant material which was carried to Hannover (Sickenberg 1968a). Part of the material, including the carnivores and the giraffids, was studied by Sickenberg and then sent back to the University of Athens (Sickenberg 1967, 1968b). The rest material remained in Hannover till 1992. At that time one of us (G. Koufos) asked from the University of Hannover to send back the material. The director of the laboratory in Hannover, Prof. Becker-Platten, sent back immediately to our laboratory the material in his disposal. This material was prepared and registered again. The artiodactyls (bovids and cervids) were given by G. Koufos to D. Kostopoulos and have been studied by him as a part of his thesis (Kostopoulos 1996). The rest material, including the equids, is studied in this article.

The locality is situated near the village of Volax about 11 km north-west of Drama (Fig. 1) in a small karstic-tectonic basin. The basin is filled by clastic sediments belonging to two alluvial fans. The deposits consist of alternating beds of conglomerates and calcareous sandstones with lenticular intercalations of very hard calcitic-arenaceous clays including the fossils. Two fossiliferous sites have been found, referred as Lager 1 and Lager 2 (Sickenberg 1968a). Both sites are situated in Leprokatia ravine; Lager 2 is located at the eastern wall of the ravine and Lager 1 at the western wall, about 3-5 m above Lager 2 (Kostopoulos 1996). The matrix is very hard and the preparation of the fossils quite difficult. The material from both sites was mixed by Sickenberg and for this reason it will be referred as a single sample under the locality indication "Volax" (VOL).

The Volax material includes quite well preserved specimens of equids which allow a good description and comparison with the known

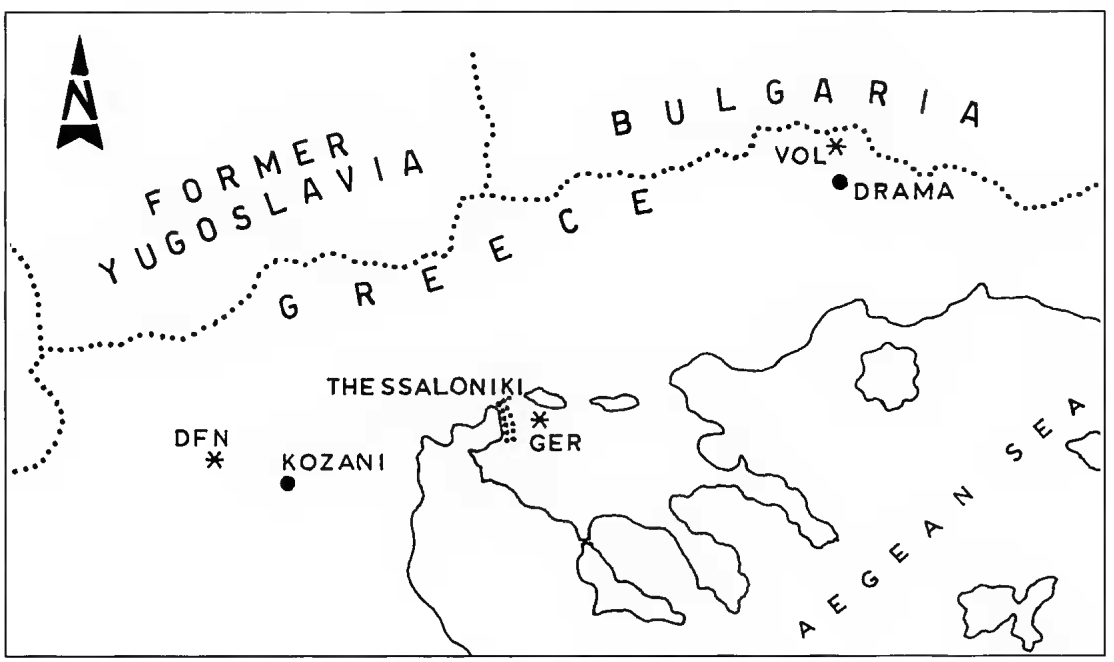

FIG. 1. — Sketch map indicating the various referred Villafranchian localities of Macedonia, Greece.

Villafranchian horses of Greece and Europe: Some years ago the Villafranchian equids of Greece were more or less unknown. Recently a rich sample from the various localities of Mygdonia basin (Macedonia, Greece) has been described (Koufos 1992; Koufos *et al.* in prep.). Some material of Villafranchian horses was also described from western Macedonia, Greece (Steensma 1988; Koufos & Kostopoulos 1993). Moreover some equids are also reported from the Villafranchian locality of Sesklon (Thessaly, Greece) by Symeonidis (1991-1992). The study of the Volax equids will add to our knowledge about the Villafranchian horses and their relationships, as well as to the biostratigraphy of Villafranchian.
The descriptions and measurements of the material are given according to the system proposed by Eisenmann *et al.* (1988).

PALAEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Genus *Equus* Linneaus, 1758
Species ***Equus stenonis*** Cocchi, 1867

Equus stenonis cf. *vireti*

LOCALITY. — "Volax", VOL (= Lager 1 and 2 of Sickenberg 1968a), Macedonia, Greece.

AGE. — Middle Villafranchian (late Pliocene).

MATERIAL. — Maxilla with P2-M3 dex and P2-M2 sin, VOL-203; P2 dex, VOL-209; P3,4 sin, VOL-207; M3 sin, VOL-208; mandible, VOL-202; right mandibular ramus with dp2-dp4, VOL-204; 5 distal parts of humerus, VOL-172, 173, 174, 175, 177; radius, VOL-170; proximal part of radius, VOL-169; 2 distal parts of radius, VOL-167, 168; 2 Mc III, VOL-152, 155; proximal part of Mc III, VOL-157; 2 distal parts of Mc III, VOL-153, 156; tibia, VOL-162; 2 proximal parts of tibia, VOL-163, 165; 4 distal parts of tibia, VOL-160, 161, 164, 166; os cuboid, VOL-198; 2 astragali, VOL-167, 169; 2 Mt III, VOL-145, 149; 3 proximal parts of Mt III, VOL-144, 146, 147; 5 distal parts of Mt III, VOL-148, 150, 154, 158, 159; first anterior phalanx, VOL-183; first posterior phalanx, VOL-181; proximal part of first phalanx, VOL-184; 2 distal parts of first phalanx, VOL-182, 185; 2 second phalanges, VOL-186, 187; 4 third phalanges, VOL-188, 189, 190, 191.

DESCRIPTION

Maxilla and mandible

A maxilla (Fig. 2) is only known with both toothrows and a more or less complete mandible (Fig. 3) without the ascending ramus. The palate is relatively elongated, narrow and deep. The distance anterior border of P2-choanae is 148 mm, while the palatal breadth is 73.4 mm in front of P2 and 75.5 mm between the posterior borders of P4. The choanae are broad and their anterior border is situated at the middle of M2. The facial crest is strong and its anterior border is situated above M1. The toothrow length is 185 mm and the length of the premolar and molar rows is 102 mm and 83.6 mm respectively. The index Molar length × 100/Premolar length is 83.6 *vs* 88.6 for *E. s.* cf. *vireti* (Dafnero, western Macedonia, Greece), 84.2 for *E. s. mygdoniensis* (Gerakarou, Mygdonia basin, Macedonia, Greece), 84.1 for *E. s.* cf. *vireti* (La Puebla, Spain), 82.7 for *E. s. vireti* (Saint-Vallier, France), 80 for *E. s. senezensis* (Seneze, France) and 76.9-86.2 for *E. s. stenonis* from U. Valdarno; data from Prat (1968), Eisenmann (1980), Privat Defaus (1986), Koufos (1992), and Koufos & Kostopoulos (1993). The Volax horse in this character is similar to the stenonoid horses. In front of P2 there is the trace of a small single-rooted dP1.
The mandible is large and elongated with relatively shallow horizontal ramus. The snout is relatively long and narrow; however at the incisor's area it is wide. The symphysis is elongated. There is not any trace of dp1. The toothrow length is 188.5 mm, while that of the premolars and molars is 92.2-98.3 mm and 91.5 mm respectively. The index Molar length × 100/Premolar length is 93.6 *vs* 92.6 for *E. s.* cf. *vireti* (Dafnero, western Macedonia, Greece), 95.6 for *E. s. mygdoniensis* (Gerakarou, Mygdonia basin, Macedonia, Greece), 92.3 for *E. s. senezensis* (Senèze, France) and 90.3-96.6 for *E. s. stenonis* from U. Valdarno; data from Prat (1968), Privat Defaus (1986), Koufos (1992) and Koufos & Kostopoulos (1993).

Permanent dentition

The upper teeth are small relatively to the skull with strong mesostyle.

The fossettes are always closed and isolated. The enamel in their borders is slightly plicated. In the very worn teeth (VOL-209) the enamel is simple and the fossettes are buccolingually narrow. The plication number is as an average five plis in the premolars and six plis in the molars. The protocone is assymetrical and relatively short with flat lingual border. In the premolars it is triangular, while in the molars it is more elongated and elliptical. In the extremely worn P2 (VOL-209) the protocone is rounded. The short protocone characterizes *E. stenonis* (Azzaroli 1965; De Giuli 1972). The pli cabalin is simple and small or rudimentary. The hypocone is elliptical with rounded distolabial border. The distal hypoconal groove is narrow and shallow, while a slight lingual groove is present only in the premolars. In M3 there is one isolated hypoconal islet. There are no unworn or little worn teeth to measure the hypsodonty but from the available material the teeth seem to be hypsodont.

The lower incisors are medium-sized with elliptical-rounded crowns and well developed cusps. The paraconid is moderately developed in p2. The parastylid is moderately developed; its lingual border does not exceed the middle of the metaconid. It is also closed from all sides, suggesting a "stenonine" type horse (Eisenmann 1981, fig. 3).

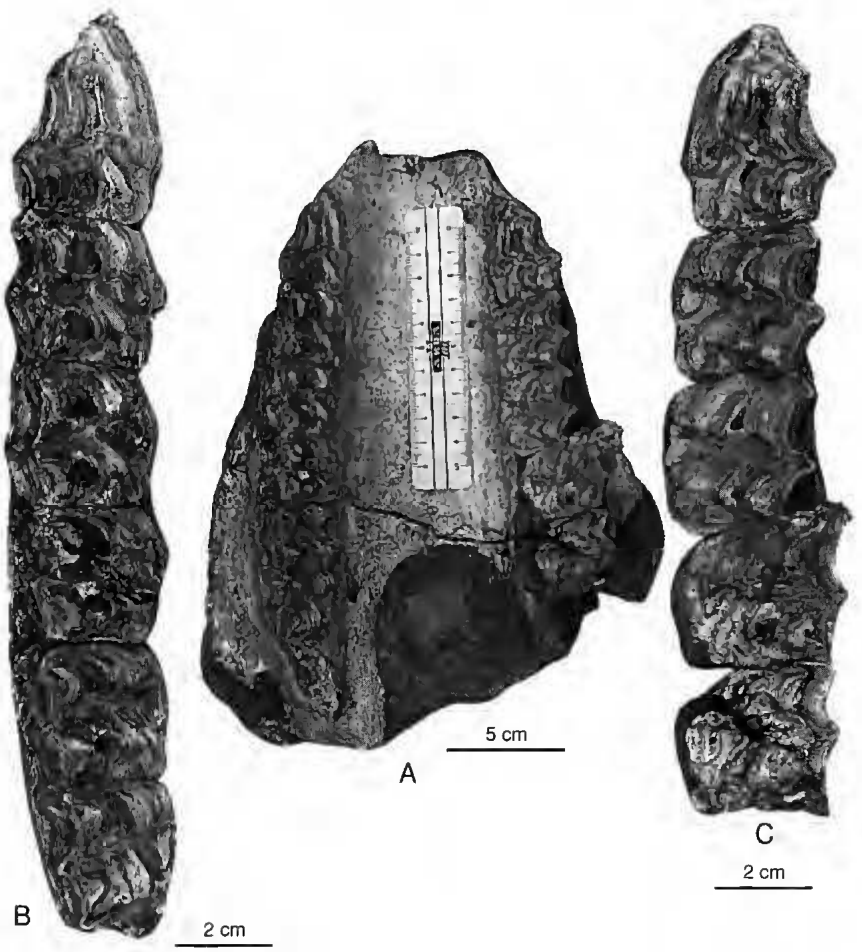

FIG. 2. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. **A**, maxilla with P2-M3 dex and P2-M2 sin, VOL-203; **B**, right toothrow of the maxilla VOL-203; **C**, left toothrow of the maxilla VOL-203.

The metaconid is rounded, the metastylid elliptical-rounded and the entoconid squarish in the premolars and elliptical in the molars. The lingual wall of both metaconid and metastylid is convex. The linguaflexid is V-shaped and deep, like in the "stenonine" type horses (Azzaroli 1965; De Giuli 1972; Eisenmann 1981). The linguaflexid is shallower in the premolars than in the molars; in the latter it sometimes touches the ectoflexid. The latter is V-shaped, open and shallow in the premolars but deeper and narrower in the molars. There is a simple and very small rudimentary pli caballinid which tends to disappear in the more worn teeth (m1 of VOL-208). The enamel at the preflexid' borders is simple, while the postflexid has plicated or crenulated enamel in its buccal border.

Milk dentition

A unique complete lower milk tooth row with slightly worn teeth is available. The paraconid in dp2 is moderately developed. The parastylid in dp3,4 is well developed and closed. The enamel at the flexid's borders is simple, without plications. The linguaflexid has open-V shape, while

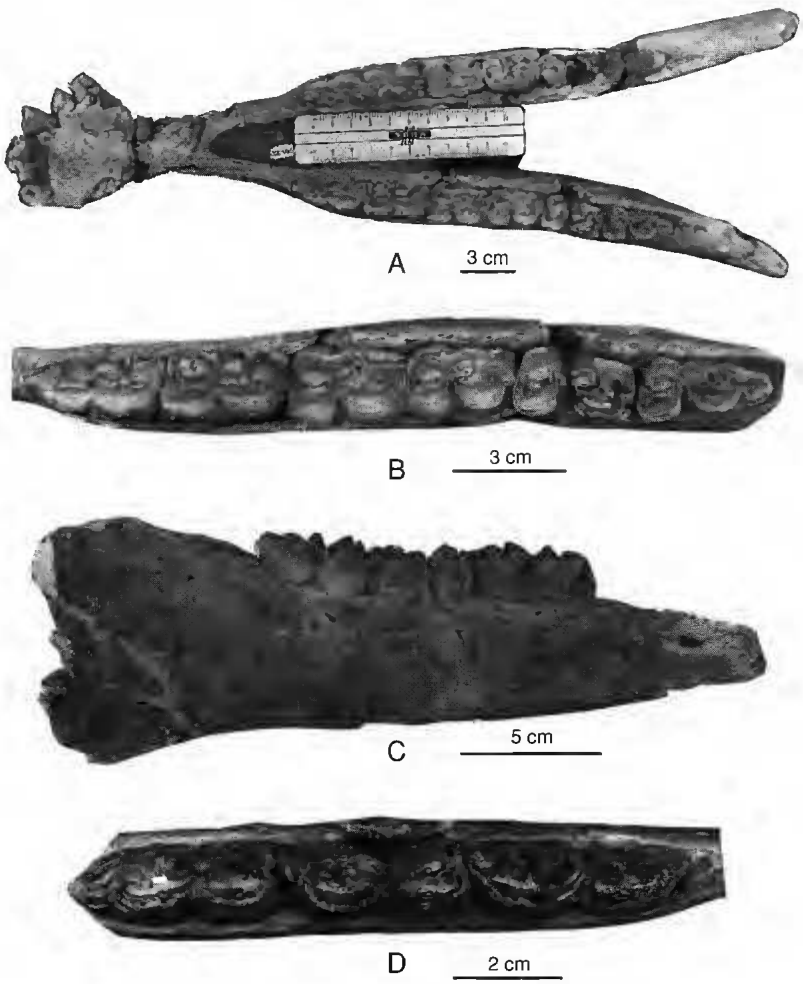

FIG. 3. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. **A**, mandible with both toothrows, VOL-202; **B**, left toothrow of the mandible VOL-202; **C**, right mandibular ramus with dp2-dp4, VOL-204; **D**, right milk toothrow of the mandible VOL-204.

the ectoflexid is narrow, U-shaped and touches the linguaflexid. The metaconid, metastylid and entoconid are little worn and their shape is asymmetrical. The hypoconulid is well developed; in dp3 it is separated as an islet. There is no trace of ectostylid. In front of dp2 there is the alveole of a very small dp1.

Postcranials

The postcranials are few and badly preserved. Nevertheless, there are some complete metapodials, phalanges and some tarsals.

Metacarpals. These are short and robust. The index height Mc III × 100/height Radius is 66.5 and suggests a short metacarpal. The slenderness

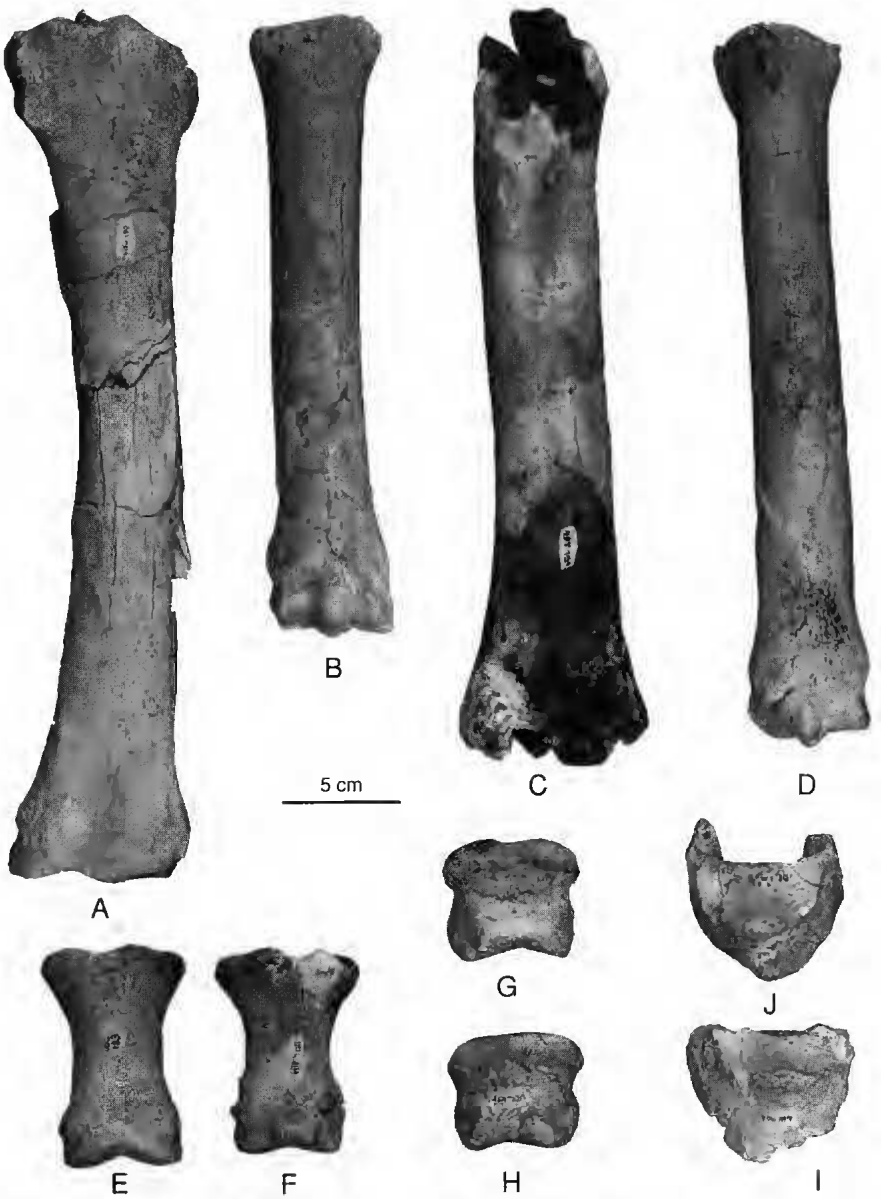

FIG. 4. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. **A**, radius, VOL-170; **B**, third metacarpal, VOL-155; **C**, distal part of tibia, VOL-164; **D**, third metatarsal, VOL-149; **E**, phalanx I anterior, VOL-183; **F**, phalanx I posterior, VOL-181; **G**, phalanx II, VOL-186; **H**, phalanx II, VOL-187; **I**, phalanx III, VOL-189; **J**, phalanx III, VOL-191.

index (= distal articular breadth × 100/height) is 20.1, indicating a relatively robust metapodial. The keel index (= distal articular breadth × 100/max DAP of the keel) is 129.9, indicating a moderately developed keel. In the available metacarpals there is no fusion of the lateral metapodials with the central one, the proximal part is flattened and the anteroposterior diameter of the proximal articular facet is short. The suprarticular fossae are sharp in the anterior face of the distal part with various depth, while in the posterior face the keel is not very high. All these features of the metacarpals are characteristic for the stenonoid horses (Gromova 1949; De Giuli 1972).

Metatarsals. These are short and robust; the slenderness index is 17, indicating a robust metatarsal. Morphologically, in the posterior surface of the distal part, there are two fossae separated by a slight crest indicating a stenonoid horse (De Giuli 1972). In the stenonoid horses the metatarsals relative to the metacarpals are shorter (De Giuli 1972). The index height Mc III × 100/height Mt III is 87.6, *vs* 84.2 for DFN, 86.5 for La Puebla, 87.8 for Saint-Vallier, 86.5 for Olivola and 87.5-89 for Gerakarou horse. According to this character the Volax equid belongs to the stenonoid horses, as this index for *E. caballus* is 82 (De Giuli 1972).

Astragali. The two available astragali from Volax have higher than 100 index height of the lateral condyle × 100/max breadth; this index is at mean 105 for the Volax equid, while in the caballoid populations it is 96.3 (De Giuli 1972). The crest distinguishing the facets for navicular and cuboid is very sharp and the facet for cuboid is very oblique. These two morphological features suggest a stenonoid horse (Gromova 1949; De Giuli 1972).

First phalanges. These are relatively short and robust; the anterior first phalanx is slenderer than the posterior one. The trigonum phalangis is relatively short; the index max length of trigonum phalangis × 100/height is 56.1 *vs* 70-74 for the caballoid horses (De Giuli 1972). Thus, in this feature, the Volax horse is similar to the stenonoid horses. The second phalanges are short, robust and anteroposteriorly flattened.

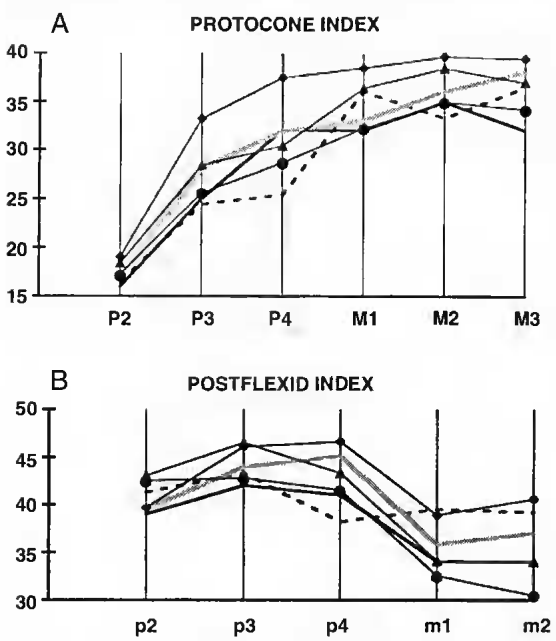

FIG. 5. — Comparative diagram of Protocone index (A) and Postflexid index (B) for the teeth of various stenonoid horses. –, *E. s.* cf. *vireti*, Volax, VOL; –, *E. s* cf. *vireti*, Dafnero, Greece (Koufos & Kostopoulos 1993); , *E. s.* cf. *vireti*, La Puebla, Spain (Eisenmann 1980, 1981); ◆, *E. s. vireti*, Saint-Vallier, France (Eisenmann 1980, 1981); ▲, *E. s. senezensis*, Senèze, France (Eisenmann 1980, 1981); ●, *E. s. mygdoniensis*, Gerakarou, Greece (Koufos 1992).

DISCUSSION

As referred in the description, the Volax equid has dental and postcranial morphology and proportions similar to those of *E. stenonis*. However there are several subspecies of *E. stenonis* described from various European localities. Two well known subspecies are known from Macedonia: *E. s.* cf. *vireti* from the locality of "Dafnero" (DFN), western Macedonia, Greece (Koufos & Kostopoulos 1993), and *E. s. mygdoniensis* from the locality of "Gera-karou-1" (GER), Mygdonia basin, Macedonia, Greece (Koufos 1992). A stenonoid horse referred as *E. stenonis* is known from Thessaly (Symeonidis 1991-1992). A small-sized stenonoid horse similar to that from Gerakarou is also referred from the Grevena basin as *E. s.* cf. *senezensis* (Steensma 1988). Besides these Greek subspecies there are several others known from the Villafranchian of Italy, France and Spain. The Volax equid will be com-

pared with these in order to find its relationships with them.

The Dafnero horse is a stenonoid one which has great similarities with that from Volax. It is a large-sized horse with moderately plicated enamel in the upper teeth (an average of six plis in the premolars and 6.4 plis in the molars), short protocone with flat lingual border, hypsodont teeth, slightly plicated flexids in the lower teeth, short and robust metapodials (Koufos & Kostopoulos 1993). The protocone index (Fig. 5A) of Volax and Dafnero horse is more or less similar, while the postflexid index (Fig. 5B) of the Dafnero horse is high, suggesting longer postflexid. As the postflexid length depends upon the attrition, and as the specimens from Volax are few (1-2), this difference is possibly not valid. The Volax metapodials are very similar to those of Dafnero (Fig. 6A). In the diagrams of figure 6 their lines are parallel to those of Dafnero horse, suggesting similar size and proportions. Moreover their general proportions are similar to those of the large stenonoid horses confirming their determination to *E. stenonis*. Similar results are also taken from the comparison of the first phalanges (Fig. 7). Thus the horse from Volax is similar to that from the middle Villafranchian locality of DFN and both can belong to the same subspecies.

Another stenonoid horse is known from the locality of Sesklon (Thessaly, Greece). It has large dimensions; the length of the lower toothrow is 191 mm (Symeonidis 1991, 1992). The size of the first phalanges and astragalus are very close to those of the VOL equid. Unfortunately there are no measurements from the metapodials for a comparison with the studied ones; the material of Sesklon is still on study. However from the few available data the Sesklon horse seems to be very close to those of Volax and Dafnero.

The horse of La Puebla (Spain), referred as *E. s.* cf. *vireti*, is a large-sized stenonoid horse, similar to the studied one. The upper toothrow length is 191 mm (Eisenmann 1980) *vs* 185 mm for the Volax equid. The protocone index of the Volax equid is similar to that of the La Puebla horse; only the protocone index of P3 and M3 from Volax is smaller than that of La Puebla (Fig. 5A). The postflexid index of the Volax horse is smaller in p4 and m1,2 than that of La Puebla (Fig. 5B). But as the Volax material is very scanty comparatively to that of La Puebla, this difference is not sufficiently proved. The metapodials and first phalanges of the Volax horse fit very well with those of La Puebla; their size and proportions are the same (Fig. 6). Moreover the various indices calculated for the metapodials of the Volax horse are similar to those for the La Puebla one (see description). Taking in account all the above data, the Volax and La Puebla equids are similar and can be determined to the same subspecies.

The subspecies *E. s. vireti* is known from the locality of Saint-Vallier (France). It is larger than

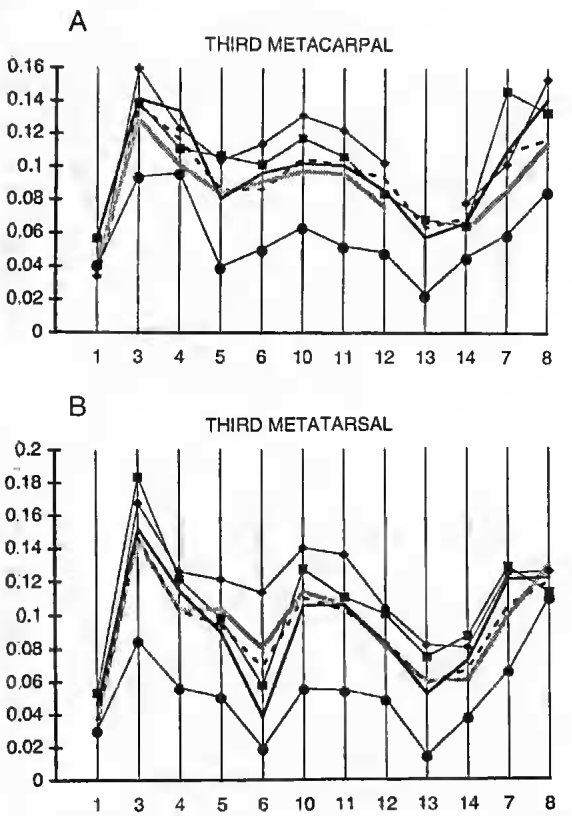

FIG. 6. — Logarithmic ratio diagram comparing the metapodials of the Volax equid with those of *E. stenonis* from various localities. Standard *E. hemionus onager* (Eisenmann & Beckouche 1986). –, *E. s.* cf. *vireti*, Volax, VOL; --, *E. s.* cf. *vireti*, Dafnero, Greece (Koufos & Kostopoulos 1993); . . , *E. s.* cf. *vireti*, La Puebla, Spain (Eisenmann 1979); ◆, *E. s. vireti*, Saint-Vallier, France (Eisenmann 1979); ●, *E. s. mygdoniensis*, Gerakarou, Greece (Koufos 1992); ■, *E. s. stenonis*, Olivola, Italy (De Giuli 1972).

the Volax horse with relatively higher protocone and postflexid indices except those of P2 and p2 (Fig. 5). The toothrow length is 182-196 mm (mean 197.5 mm) for the upper and 176-199 mm (mean 190 mm) for the lower jaw (Prat 1968). The toothrow length of the Volax horse is into the ranges of variation for *E. s. vireti* but its mean values are slightly smaller than those of Saint-Vallier. However the metapodials of *E. s. vireti* have similar height with those from Volax but their proportions are larger, indicating slightly more robust metapodials than those of Volax (Fig. 6). This difference is clearer in the metatarsals. The first phalanx of *E. s. vireti* is also larger than that of Volax (Fig. 7). Considering all these characters the Volax equid has great similarities with the type material of *E. s. vireti* but it is slightly smaller with slightly slenderer metapodials.

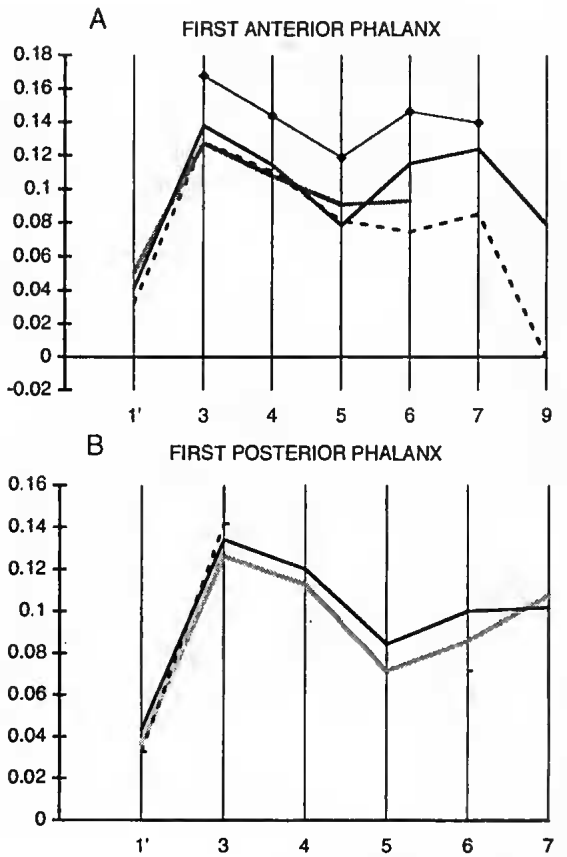

FIG. 7. — Logarithmic ratio diagram comparing the first phalanges of the Volax equid with those of *E. stenonis* from various localities. Standard *E. hemionus onager* (Eisenmann & De Giuli 1974; Dive & Eisenmann 1991). –, *E. s.* cf. *vireti*, Volax, VOL; –, *E.* s. cf. *vireti*, Dafnero, Greece (Koufos & Kostopoulos 1993); –, *E. s.* cf. *vireti*, La Puebla, Spain (Eisenmann 1979). ◆, *E. s. vireti*, Saint-Vallier, France (Eisenmann 1979).

The typical subspecies *E. s. stenonis* is known from the area of Tuscany, Italy (Valdarno, Olivola, Matassino). A good description of this subspecies is given for the material of Olivola and Matassino by De Giuli (1972). The tooth-row length is 187-189 mm for the upper and 194-195 mm for the lower jaw; these values are close to those of the Volax sample. The metapodials from Olivola have slightly larger dimensions than those of Volax, Dafnero and La Puebla, situated between them and *E. s. vireti* from Saint-Vallier (Fig. 6). The maximal diameter of the articular facet for the os magnum in Mc III is significantly longer in the Olivola sample than in the others (measurement 7 in Fig. 6A). The diaphysis is wider in the Olivola metatarsals than in the other horses (measurement 3 in Fig. 6B). *E. s. stenonis* is not very different from *E. s. vireti*; their skull size is similar but *E. s. stenonis* has longer metapodials (Azzaroli 1990). The comparison of the metapodials (Fig. 6) suggests that their general proportions are very similar.

All the European subspecies of *E. stenonis* are based on differences in the size and proportions representing geographical and/or chronological varieties. Sometimes the few available or fragmentary material cannot allow a good statistical analysis evidencing some differences. Three possibilities can be proposed for these large horses of the end of Pliocene: (a) to represent a single subspecies of *E. stenonis* with local varieties; (b) to represent two subspecies, *E. s. vireti* (La Puebla, Dafnero, Volax) and *E. s. stenonis* (Valdarno, Olivola, Matassino); and (c) to include Dafnero, Volax and La Puebla to a new subspecies. The first hypothesis seems to be the most probable but since I have not seen all this material I cannot support it at the moment; a monography revising all European stenonoid horses is necessary in order to clarify their relationships and to define the valuable species and subspecies.

From the Villafranchian localities of Mygdonia basin (Macedonia, Greece), a stenonoid horse has

been described as *E. s. mygdoniensis*; the better sample is that of the locality of "Gerakarou 1", GER (Koufos 1992). *E. s. mygdoniensis* is smaller, with relatively slenderer metapodials than the Volax horse. The toothrow length is 173.5 mm for the upper and 167.8 mm for the lower jaw *vs* 185 mm and 188.5 mm for the Volax horse respectively. The slenderness index is 18.6 for Mc III and 15.9 for Mt III, while in the Volax horse it is respectively 20.1 and 17. The metapodials of the Gerakarou horse have more or less similar height but their relative proportions are quite smaller than those of the studied equid (Fig. 6). The horse found in the locality of Livakos (Grevena basin) and described as *E. s.* cf. *senezensis* (Steensma 1988) is smaller than that of Volax and closer to *E. s. mygdoniensis* (Koufos 1992).
Concerning all the above mentioned descriptive and comparative data, the Volax horse belongs to *E. stenonis* and has greatest similarities with the forms from Dafnero and La Puebla. It is also close to *E. s. vireti* from Saint-Vallier. It has as well some similarities to *E. s. stenonis* from Olivola and Matassino. Thus, the Volax horse is referred as *E. s.* cf. *vireti*.

BIOCHRONOLOGY

The Volax horse belongs to the large-sized stenonoid horses which appeared at the end of Pliocene. The oldest representative of *Equus* in Europe is *E. livenzovensis* while the first appearence of the genus in Eurasia has been dated at about 2.5 Ma (Lindsay *et al.* 1980; Bonadonna & Alberdi 1987). *E. stenonis* including the late Pliocene-early Pleistocene horses with several forms, allowed the subdivision of that time span (Bonadonna & Alberdi 1987; Azzaroli 1990). The Volax horse has some similarities with *E. s. vireti* from Saint-Vallier. The Saint-Vallier locality has been dated to late Pliocene, MN17 (Mein 1990). According to Torre *et al.* (1992) the Saint-Vallier locality belongs to the Saint-Vallier Faunal Unit corresponding to the end of middle Villafranchian. The horse of Volax is very similar to that of Dafnero (Greece) and La Puebla (Spain). The Dafnero locality has been dated to middle Villafranchian (zone MN17a of Mein 1990; or MNQ17 of Guerin 1990), (Koufos *et al.* 1991; Koufos 1993; Koufos & Kostopoulos 1993; Kostopoulos & Koufos 1994; Kostopoulos 1996). The locality of La Puebla is also dated to middle Villafranchian, MN17 and is considered slightly younger than that of Saint-Vallier (Mein 1990). Taking into account the above mentioned similarities of the Volax horse with those from

FAUNA	VOL	DFN	PUE	STV	OLI
Macaca cf. *florentina*			sp.	+	
Paradolichopithecus arvernensis			+		
Anancus arvernensis				+	
Archidiskodon meridionalis			+	+	+
Elephantidae indet.	+				
Nyctereutes megamastoides	+	+	+	+	
Vulpes alopecoides		+	+	+	
Vulpes praecorsac	+				
Canis cf. *falconeri*			+		
Canis etruscus					+
Ursus etruscus		+	+	+	+
Bosdagius felinus	+				
Pliohyaena perrieri			+	+	
Pliohyaena brevirostris					+
Baranogale helbingi		cf.	+		
Chasmaporthetes lunensis		+	+	+	+
Meganlereon megantereon	+		+	+	+
Lynx issiodorensis	?			+	+
Acinonyx pardinensis			+	+	+
Panthera schaubi			cf.	+	
Panthera gombaszoegensis					+
Meles thorali				+	
Enhydrictis ardea				+	+
Homotherium sainzelli				+	
Homotherium crenatidens					+
Equus stenonis vireti	cf.	cf.	cf.	+	
Equus stenonis stenonis					+
Dicerorhinus etruscus			+	+	+
Rhinocerotidae indet.	+				
Sus strozzii					+
Mitilanotherium martinii	+	+			
Eucladoceros senezensis	+	+	+	+	
Eucladoceros dicranios					+
"Cervus" philisi	+	+	+	+	
Croizetoceros ramosus	+		+	+	
Leptobos stenometopon				+	
Leprobos etruscus					+
Leptobos	cf.				
Gazelliospira torticornis	cf.	+	+	+	
Gallogoral meneghinii	+	cf.	cf.	+	+
Gazella bouvrainn.sp.	sp.	+			
Gazella borbonica			+	+	
Procamptoceras brivatense	? sp.				+
Antilopinae indet.		+			

FIG 8. — Faunal list: **VO**, Volax (Sickenberg 1967, 1968a, b; Kostopoulos 1996); **DFN**, Dafnero (Koufos 1993; Koufos & Kostopoulos 1993, 1997; Kostopoulos 1996); **PUE**, La Puebla (Aguirre & Morales 1990), **STV**, Saint-Vallier (Heintz *et al.* 1974); **OLI**, Olivola.

Simpson's Index	VOL		DFN		PUE		STV		OLI	
VOL	100	100	75	62	77	63	85	63	39	31
DFN			100	100	91	69	83	69	41	23
PUE					100	100	86	90	57	35
STV							100	100	88	45
OLI									100	100

Pickford's Index	VOL		DFN		PUE		STV		OLI	
VOL	0	0	8	19	8	23	85	63	43	52
DFN			0	0	4	18	10	14	41	65
PUE					0	0	6	3	13	43
STV							0	0	4	36
OLI									0	0

FIG. 9. — Faunal similarities indices of Simpson and Pickford, calculated for the localities of figure 8. The left number is at generic level and the right number at specific level.

the other localities, a similar age can be proposed for the locality of Volax.

The material collected from Volax has been determined by Sickenberg (1967, 1968a, b) and the following species are referred: *Megantereon megantereon megantereon*, *Nyctereutes megamastoides megamastoides*, *Vulpes praecorsac*, *Bosdagius felinus*, *Felis* (*Lynx*) *issiodorensis*?, *Macedonitherium martinii*, *Leptobos* sp., *Nemorhedus* sp., *Gazella* sp., *Gazellospira* sp., *Didermoceros* sp., *Equus* (*Allohippus*) sp. and *Proboscidea* indet., while an earliest Pleistocene age has been proposed. However the presence of *Nyctereutes* in the Volax fauna suggests an older age; the genus has been replaced by *Canis* at the beginning of late Villafranchian (Torre *et al.* 1992). Thus the Volax fauna must be older than Early Pleistocene. The recent study of the bovids and cervids from Volax (Fig. 8) and their comparison with those of the other Greek and European localities suggest also a middle Villafranchian (MN17a) age (Kostopoulos & Koufos 1994; Kostopoulos 1996). This age confirms the above mentioned age proposed for the studied equid.

As it was referred before, the Volax equid is similar or has similatities with that from Dafnero, La Puebla, Saint-Valliet and Olivola. A comparison of the whole fauna from Volax with those of the above mentioned localities is necessary to establish these similarities.The faunal composition of Volax is similar to that of Dafnero, La Puebla and Saint-Vallier (Fig. 8). The similarity index of Simpson is high, both in generic and specific level, while the distance index of Pickford is small (Fig. 9), indicating strong faunal similarities. The differences in the faunal composition are referred in the absence of some small carnivores (Fig. 8), which are difficult to be preserved pre- and post-mortem. Taxonomical problems cause also some differences in the composition of the fauna. The utsid *Bosdagius* is known only from Volax and possibly represents a form of the genus *Ursus*.

However the Olivola fauna differs more from the others and seems to be younger. The Simpson index is small and the Pickford index is high both in generic and specific level indicating the differentiation of the Olivola fauna from the others (Fig. 9). The presence of *Canis etruscus*, *Pliohyaena brevirostris* and *Panthera gombaszoegensis* indicates a younger age for the Olivola fauna. As mentioned before, *Canis etruscus* corresponds to the beginning of early Pleistocene (Torre *et al.* 1992). The large-sized *Pliohyaena brevirostris* appeared in Europe at early Pleistocene in Olivola fauna (Torre *et al.* 1992). However, in Greece, this species has appeared earlier in the Gerakarou fauna, where it was found togethet with *Pliohyaena perrieri*. The Gerakarou fauna has been dated at the transition between Pliocene/Pleistocene (Koufos 1992; Kostopoulos 1996). *Panthera gombaszoegensis* also characterizes the beginning of late Villafranchian (Azzaroli *et al.* 1988) and its presence in the

Olivola fauna indicates a younger age than that of Volax, Dafnero, La Puebla and Saint-Vallier. In the last two localities the more primitive *Panthera schaubi* is present. The Volax fauna preserves more primitive characters and corresponds to Saint-Vallier Faunal Unit of Torre *et al.* (1992). These faunal similarities of the Volax material with the other localities reflect also age similarities and a middle Villafranchian age is proposed for the locality of Volax.

Acknowledgments
We thank very much Prof. A. Azzaroli and Dr V. Eisenmann for their useful comments on the manuscripts.

REFERENCES

Aguirre E. & Morales J. 1990. — Villafranchian faunal record of Spain. *Quartärpaläontologie* 8: 7-11.

Azzaroli A. 1965. — The two Villafranchian horses of the Upper Valdarno. *Paleontographia Italica* 59: 1-12.

— 1990. — The genus *Equus* in Europe: 321-356, *in* Lindsay E. H., Fahlbusch V. & Mein P. (eds), *European Neogene Mammal Chronology*. Plenum Press.

Azzaroli A., De Giuli C., Ficcarelli G. & Torre D. 1988. — Late Pliocene to early mid-Pleistocene mammalian faunas in Eurasia: Faunal succession and dispersal events. *Palaeogeography, Palaeoecology, Palaeoclimatology* 66: 77-100.

Bonadonna P. F. & Alberdi M.-T. 1987. — *Equus stenonis* Cocchi as a biostratigraphical marker in the Neogene-Quaternary of the western Mediterranean basin: Consequence on Galerian-Villafranchian Chronostratigraphy. *Quaternary Science Review* 6: 55-66.

De Giuli C. 1972. — On the type form of *Equus stenonis* Cocchi. *Paleontographia Italica* 38: 35-49.

Dive J. & Eisenmann V. 1991. — Identification and discrimination of first phalanges from Pleistocene and modern *Equus*, wild and domestic: 279-333, *in* Meadow R. H. & Uerpmann H.-P. (eds), *Equids in the ancient world*. Dr L. R. Verlag.

Eisenmann V. 1979. — Les métapodes d'*Equus* s. l. (Mammalia, Perissodactyla). *Geobios* 12 : 863-886.

— 1980. — Les chevaux (*Equus* sensu lato) fossiles et actuels. Crânes et dents jugales supérieures. *Cahiers de Paléontologie* : 1-186.

— 1981. — Étude des dents jugales inférieures des *Equus* (Mammalia, Perissodactyla) actuels et fossiles. *Palaeovertebrata* 10 : 1-226.

Eisenmann V. & Beckouche S. 1986. — Identification and discrimination of metapodials from Pleistocene and modern *Equus*, wild and domestic: 117-163, *in* Meadow R. H. & Uerpmann H.-P. (eds), *Equids in the ancient world*. Dr L. R. Verlag.

Eisenmann V. & De Giuli C. 1974. — Caractères distinctifs des premières phalanges antérieures et postérieures chez certain équidés actuels et fossiles. *Bulletin de la Société Géologique de France*, 7e ser. 26 : 352-361.

Eisenmann V., Alberdi M.-T., De Giuli C. & Staesche U. 1988. — *In* Woodburne M. & Sondaar P. (eds), *Studying fossil horses*, I. Methodology: 1-70.

Gromova V. 1949. — Le genre *Equus*. *Annales du Centre d'Études et de Documentation, Paléontologie* 13 : 1-203.

Guérin C. 1990. — Biozones or mammal units? Methods and limits in biochronology: 119-130, *in* Lindsay E. H., Fahlbusch V. & Mein P. (eds), *European Neogene Mammal Chronology*. Plenum Press.

Heintz E., Guérin C., Martin R. & Prat F. 1974. — Principaux gisements villafranchiens de France : listes fauniques et biostratigraphie. *Mémoires du Bureau de Recherches Géologiques et Minières*, Paris 78 : 169-182.

Kostopoulos D. S. 1996. — *The Plio-Pleistocene artiodactyls of Macedonia, Greece. Systematics, Palaeoecology, biochronology, biostratigraphy*: 1-532. Ph. D. Thesis, University of Thessaloniki.

Kostopoulos D. S. & Koufos G. D. 1994. — The Plio-Pleistocene artiodactyls of Macedonia (Northern Greece) and their biostratigraphic significance; preliminary report. *Compte Rendus de l'Académie des Sciences*, Paris 318 : 1267-1272.

Koufos G. D. 1992. — Early Pleistocene equids from Mygdonia basin (Macedonia, Greece). *Paleontographia Italica* 79: 167-199.

— 1993. — Late Pliocene carnivores from Western Macedonia (Greece). *Paläontologische Zeitschrift* 67 (3/4): 357-376.

Koufos G. D. & Kostopoulos D. S. 1993. — A stenonoid horse (Equidae, Mammalia) from the Villafranchian of Western Macedonia (Greece). *Bulletin Geological Society of Greece* 28: 131-143.

— 1997. — Some carnivores from the Villafranchian of Macedonia, Greece with the description of a new canid. *Münchener Geowissenschaften* A34: 33-63.

Koufos G. D., Kostopoulos D. S. & Koliadimou K. K. 1991. — Un nouveau gisement de mammifères dans le Villafranchien de Macédoine occidentale (Grèce). *Comptes Rendus de l'Académie des Sciences*, Paris, série II, 313 : 831-836.

Lindsay E. H., Opdyke N. D. & Johnson N. M. 1979. — Pliocene dispersal of the horse *Equus* and late cenozoic mammalian dispersal events. *Nature* 287: 135-138.

Mein P. 1990. — Updating of MN Zones: 73-90, *in*

Lindsay E. H., Fahlbusch V. & Mein P. (eds), *European Neogene Mammal Chronology*. Plenum Press.

Prat F. 1968. — *Recherches sur les équidés pleistocènes en France*. Thèse de Doctorat d'État, Université de Bordeaux : 1-325.

Sickenberg O. 1967. — Die unterpleistozäne Fauna von Wolaks (Griech. Mazedonien). 1. Eine neue giraffe (*Macedonitherium martinii* nov. gen. nov. spec.) aus dem unteren Pleistozän von Griechenland. *Annales de Géologie des Pays Helléniques* 18 : 314-330.

— 1968a. — Die pleistozänen knochenbrekzien von Volax (Griech. Mazedonien). *Geologische Jahrbuch* 85: 33-54.

— 1968b.— Die unterpleistozäne fauna von Wolaks (Griech. Mazedonien). II. Die Carnivoren. *Annales de Géologie des Pays Helléniques* 19 : 621-646.

Steensma J. J. 1988. — *Plio-Pleistozäne Grossäugetiere (Mammalia) aus dem Becken von Kastoria-Grevena, südlich von Neapolis-NW Griechenland*: 1-315. Ph. D. Thesis Technischen Universität Clausthal.

Symeonidis N. 1991-1992. — Fossilized mammals of early Pleistocene (Villafranchian) age from the basin of Sesklon (Volos). *Annales de Géologie des Pays Helléniques* 35 : 1-42.

Torre D., Ficcarelli G., Masini F., Rook L. & Sala B. 1992. — Mammal dispersal events in the early Pleistocene of Western Europe. *Courier Forschung Institut Senckenberg* 153: 51-58.

Submitted for publication on 13 May 1996;
accepted on 28 August 1996.

APPENDIX

MEASUREMENTS AND STATISTICS

Mandible	VOL-202	VOL-204*
2	~156	-
3	95.2	-
4	91.5	-
5	188.5	110.5
7	70	-
10	110	57.7
11	79.5	-
12	63.7	37.2
13	93	-
14	{24}	-
16	140	-

TABLE 1. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Mandible. *, VOL-204 is a hemimandible with milk teeth. **2**, muzzle length: middle of the line connecting the anterior borders of p2 to a point situated between the two i1; **3**, premolar length (alveolar); **4**, molar length (alveolar); **5**, toothrow length (alveolar); **7**, muzzle breadth: breadth at the posterior borders of i3; **10**, height of the jaw behind m3; **11**, *idem* between p4 and m1; **12**, *idem* in front of p2; **13**, symphysis length; **14**, minimal breadth of the symphysis; **16**, length of diastema p2-i3.

		VOL-203		VOL-209
		dex	sin	
P2	Lo	41.8	39.6	41.3
	Bo	27.8	28.0	28.2
	Lp	6.8	6.3	6.4
	Bp	5.7	5.4	5.8
	PI	16.3	15.9	15.5
P3	Lo	30.4	30.8	-
	Bo	27.3	28.7	-
	Lp	7.7	7.6	-
	Bp	6.0	5.4	-
	PI	25.3	24.7	-
P4	Lo	29.5	29.8	-
	Bo	-	29.5	-
	Lp	-	9.4	-
	Bp	-	5.2	-
	PI	-	31.5	-
M1	Lo	26.4	29.0	
	Bo	-	29.2	
	Lp	-	8.4	
	Bp	-	5.0	
	PI	-	29.0	
M2	Lo	26.9	{30.4}	
	Bo	-	27.4	
	Lp	9.6	-	
	Bp	4.4	-	
	PI	35.7	-	
M3	Lo	31.4	-	
	Bo	23.3	-	
	Lp	10.0	-	
	Bp	3.3	-	
	PI	31.8	-	

TABLE 2. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Upper permanent cheek teeth. **Lo**, occlusal length; **Bo**, occlusal breadth; **Lp**, protocone length; **Bp**, protocone breadth; **PI**, protocone index.

		VOL-202	
		dex	sin
p2	Lo	37.5	36.5
	Bo ant.	14.2	13.1
	Bo post.	16.7	17.0
	Lprfl	9.0	9.0
	Lptfl	15.0	13.5
	IF	40.0	37.0
p3	Lo	31.2	31.2
	Bo ant.	17.7	18.4
	Bo post.	17.4	19.0
	Lprfl	9.4	9.8
	Lptfl	12.4	13.4
	IF	39.7	42.9
p4	Lo	30.5	29.6
	Bo ant.	17.0	17.8
	Bo post.	17.4	19.0
	Lprfl	9.4	9.2
	Lptfl	12.2	12.6
	IF	40.0	42.6
m1	Lo	28.0	27.7
	Bo ant.	17.4	17.0
	Bo post.	16.8	18.2
	Lprfl	7.6	7.8
	Lptfl	9.0	9.8
	IF	32.1	35.4
m2	Lo	-	30.0
	Bo ant.	-	16.2
	Bo post.	-	-
	Lprfl	-	7.8
	Lptfl	-	10.1
	IF	-	33.7
m3	Lo	-	33.3
	Bo ant.	-	15.8
	Bo post.	-	13.6
	Lprfl	-	7.4
	Lptfl	-	9.4
	IF	-	28.2

TABLE 3. — *Equus stenoni* cf. *vireti*, Volax, Macedonia, Greece. Lower permanent cheek teeth. **Lo**, occlusal length; **Bo ant.**, anterior occlusal breadth; **Bo post.**, posterior occlusal breadth; **Lprfl**, preflexid length; **Lptfl**, postflexid length; **IF**, postflexid index.

Humerus	n	x	min	max	s	v
3	2	37.05	36.5	37.6	0.78	2.10
4	2	45.60	44.9	46.3	0.99	2.17
7	2	82.50	81.0	84.0	2.12	2.57
8	4	87.53	85.2	89.6	2.35	2.69
9	3	50.17	47.2	52.7	2.78	5.53
10	1	40.00	-	-	-	-
11	3	44.73	43.1	46.5	1.70	3.81

TABLE 4. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Humerus. **3**, minimal breadth (oblique); **4**, diameter perpendicular to and at the level of 3; **7**, maximal breadth of the trochlea; 8, distal maximal depth; **9**, maximal trochlear height (medial); **10**, minimal trochlear height (in the middle); **11**, trochlear height at the sagittal crest (near the condyle).

Radius	n	x	min	max	s	v
1	1	362.80	-	-	-	-
2	1	343.00	-	-	-	-
3	3	44.10	43.9	44.4	0.26	0.60
4	3	30.50	28.5	33.0	2.29	7.51
5	1	75.70	-	-	-	-
6	1	[36]	-	-	-	-
7	1	80.90	-	-	-	-
8	2	65.95	65.4	66.5	0.78	1.18
9	1	39.30	-	-	-	-
10	2	78.65	78.1	79.2	-	-
11	2	25.50	25.0	26.0	-	-
12	1	16.90	-	-	-	-

TABLE 5. — *Equus stenoni* cf. *vireti*, Volax, Macedonia, Greece. Radius. **1**, maximal length; **2**, medial length; **3**, minimal breadth of diaphysis; **4**, DAP of the diaphysis at the level of 3; **5**, proximal articular breadth; **6**, proximal articular DAP; **7**, proximal maximal breadth; **8**, distal articular breadth; **9**, distal articular DAP; **10**, distal maximal breadth; **11**, diameter of the articular facet for navicular; **12**, *idem* for triquetrum.

Mc III	n	x	min	max	*s*	v
1	2	241.45	236.4	246.5	-	-
2	1	241.70	241.7	241.7	-	-
3	2	35.85	35.5	36.2	-	-
4	2	28.70	28.3	29.1	-	-
5	1	52.00	-	-	-	-
6	1	33.80	-	-	-	-
7	1	44.00	-	-	-	-
8	1	17.00	-	-	-	-
9	1	7.50	-	-	-	-
10	3	48.93	47.4	50.0	1.12	2.27
11	4	48.55	47.4	49.7	1.10	2.27
12	3	35.80	33.9	37.2	1.39	3.90
13	3	27.53	27.0	27.9	0.38	1.40
14	4	30.18	29.1	31.5	0.91	3.03
16	2	8.00	7.5	8.5	-	-

TABLE 6. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Third metacarpal. **1**, maximal length; **2**, internal length; 3, breadth of the diaphysis (in the middle); **4**, DAP, *idem* at the level of 3; **5**, proximal articular breadth; **6**, proximal articular DAP; **7**, maximal diameter of the articular facet for os magnum; **8**, diameter of the anterior facet for hamatum; **9**, diameter of the articular facet for Mc II; **10**, distal maximal supra-articular breadth; **11**, distal maximal articular breadth; **12**, distal maximal DAP of the keel; **13**, distal minimal DAP of the lateral condyle; **14**, distal maximal DAP of the medial condyle; **16**, diameter for the articular facet for Mc III.

Tibia	n	x	min	max	s	v
3	3	46.80	45.4	47.7	1.00	2.14
4	3	32.63	31.3	33.5	0.96	2.93
5	1	74.1	-	-	-	-
6	1	61.1	-	-	-	-
7	3	71.23	68.5	75.9	3.32	4.66
8	3	47.00	44.3	49.2	2.03	4.32
9	1	17.0	-	-	-	-

TABLE 7. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Tibia. 3, minimal breadth of the diaphysis; **4**, DAP of the diaphysis at the level of 3; **5**, proximal maximal breadth; 6, proximal maximal depth; **7**, maximal distal breadth; **8**, maximal distal DAP; 9, length of the fossa digitalis.

Astragalus	VOL-196	VOL-197
1	-	65.8
2	-	[63.2]
3	30.6	28.8
4	66	64.7
5	51.3	[55.5]
6	36	34.5
7	48.5	51

TABLE 8. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Astragalus. **1**, maximal length (height) articulation surface for navicular-top of the internal condyle; **2**, meximal diameter of the internal condyle; **3**, trochlear breadth: middle of the internal-middle of the external condyles; **4**, maximal breadth (in projection), **5**, distal articular breadth; **6**, distal articular DAP; **7**, maximal DAP of the internal condyle.

Mt III	n	x	min	max	s	v
1	2	275.50	270.0	281	-	-
3	5	35.60	33.7	37.3	1.31	3.68
4	5	32.94	31.4	34.6	1.14	3.46
5	3	49.80	47.0	52	2.55	5.13
6	2	38.25	38.0	38.5	-	-
7	2	47.50	47.4	47.6	-	-
8	5	11.50	10.7	11.9	0.47	4.12
9	1	6.4	-	-	-	-
10	6	48.70	47.3	50	1.11	2.29
11	6	47.65	46.2	49.5	1.31	2.75
12	7	36.44	34.5	37.9	1.16	3.2
13	6	26.72	25.4	27.5	0.82	3.08
14	5	30.94	29.3	31.7	0.97	3.12

TABLE 9. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Third metatarsal. **1**, maximal length; **3**, breadth of the diaphysis (in the middle); **4**, DAP *idem* at the level of 3; **5**, proximal articular breadth; **6**, proximal articular DAP; **7**, maximal diameter of the articular facet for the cuneiform; **8**, diameter of the articular facet for cuboid; **9**, *idem* for cuneiform II; **10**, distal maximal supra-articular breadth; **11**, distal maximal articular breadth; **12**, distal maximal DAP of the keel; **13**, distal minimal DAP of the lateral condyle; **14**, distal maximal DAP of the medial condyle.

Phalanx I	VOL-181	VOL-182	VOL-183	VOL-184	VOL-185
1	78.4	-	84.6	-	81.8
2	71.4	-	74.9	-	-
3	32.5	-	33.5	-	34.2
4	55,7	-	54.2	44.7	54.6
5	37.0	-	37.4	29.3	-
6	44.1	43.0	46.2	-	47.1
7	42.1	-	45.0	-	46.4
8	23.7	-	24.4	-	25.2
9	42.0	-	50.1	-	45.5

TABLE 10. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. First phalanx of the third digit. **1**, maximal length; **2**, anterior length: middle of the proximal articular facet-middle of the distal facet; **3**, minimal breadth of the diaphysis; **4**, proximal breadth; 5, proximal DAP; **6**, distal breadth at the tuberosities; **7**, distal articular breadth; **8**, distal articular DAP; **9**, minimal length of the trigonum phalangis.

Phalanx II	VOL-186	VOL-187
1	48.6	46.7
2	34.3	33.2
3	45.4	45.2
4	53.8	52.2
5	33.6	32.7
6	49.5	48.1

TABLE 11. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Second phalanx of the third digit. **1**, maximal length; **2**, anterior length (as in the first phalanx); **3**, minimal breadth of the diaphysis; **4**, maximal proximal breadth; **5**, proximal DAP; 6, distal articular maximal breadth.

Phalanx III	VOL-188	VOL-189	VOL-190	VOL-191
1	57.3	47.8	-	55.7
2	47.8	50.5	-	49.8
3	67.3	67.3	-	-
6	37.1	41.4	38.8	40.8

TABLE 12. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Third phalanx of the third digit. **1**, length from the posterior edge of the articular surface to the tip of the phalanx; **2**, anterior length; 3, maximal breadth; 6, maximal height.